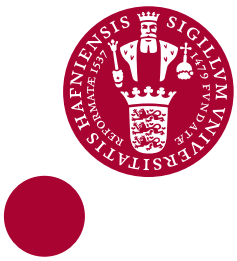

Salt acclimation induced salt tolerance is enhanced by abscisic acid priming in wheat

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Salt acclimation induced salt tolerance is enhanced by abscisic acid priming in wheat

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ABSTRACT

Wang Z.S., Li X.N., Zhu X.C., Liu S.Q., Song F.B., Liu F.L., Wang Y., Qi X.N., Wang F.H., Zuo Z.Y., Duan P.Z., Yang A.Z., Cai J., Jiang D. (2017): Salt acclimation induced salt tolerance is enhanced by abscisic acid priming in wheat. Plant Soil Environ., 63: 307–314.

High salt stress significantly depresses carbon assimilation and plant growth in wheat (*Triticum aestivum* L.). Salt acclimation can enhance the tolerance of wheat plants to salt stress. Priming with abscisic acid (1 mmol ABA) was applied during the salt acclimation (30 mmol NaCl) process to investigate its effects on the tolerance of wheat to subsequent salt stress (500 mmol NaCl). The results showed that priming with ABA modulated the leaf ABA concentration to maintain better water status in salt acclimated wheat plants. Also, the ABA priming drove the antioxidant systems to protect photosynthetic electron transport in salt acclimated plants against subsequent salt stress, hence improving the carbon assimilation in wheat. It suggested that salt acclimation induced salt tolerance could be improved by abscisic acid priming in wheat.

Keywords: soil salinization; gas exchange; chlorophyll *a* fluorescence; salinity; phytohormone

Approximately 20% of the irrigated agricultural land is affected adversely by soil salinity (Upadhyay and Singh 2015). Wheat (*Triticum aestivum* L.) is moderately tolerant to salinity; its grain yield can be

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reduced by more than 60% due to soil salinity (El-Hendawy et al. 2017). The salt-induced inhibition of growth and grain yield loss is mainly related to the negative effects of high salt on photosynthesis, ion balance and water relations (Mehta et al. 2010). Photosynthesis is a process highly sensitive to changes in environmental factors (Kalaji et al. 2017). The unbalance between light energy absorbed by photosystems and energy consumed by metabolic sinks causes photodamage to photosystem (PS) II *via* the generation of reactive oxygen species (ROS) (Brestic et al. 2015, 2016). Chlorophyll *a* fluorescence analysis is a sensitive method for the detection and quantification of changes in the photosynthetic apparatus (Kalaji et al. 2017, Zivcak et al. 2017), and various chlorophyll *a* fluorescence parameters were used to evaluate the salt induced damage to PS II (Mehta et al. 2010).

Higher plants have developed several strategies to respond and adapt to salt stress and thus acquire stress tolerance, including activation of the antioxidant systems (Pandolfi et al. 2016), induction of phytohormones (abscisic acid (ABA) and ethylene) (Garcia de la Garma et al. 2015), control of the ion uptake and translocation, and adjustment of the photosynthetic processes (Janda et al. 2014, 2016). A large body of evidence has shown that an early exposure to a moderate stressor can prepare the plants more quickly or actively to respond to subsequent stress (Bruce et al. 2007, Li et al. 2015, 2016, Liu et al. 2017). The trigger for stress tolerance (i.e. the early moderate stressor) is referred to 'priming'. Janda et al. (2016) documented that acclimation with low level of salt improves the salt tolerance *via* increasing osmotic potential and enhancing activities of antioxidant enzymes and regulating related gene expressions.

As a major plant phytohormone, ABA plays important roles in numerous biological processes (Cutler et al. 2010). It also appears to be a key player in mediating the acclimation of plant to abiotic stress (Pál et al. 2011, Li et al. 2014a). For instance, accumulated evidence indicated that ABA accumulation helps to maintain high cytosolic K^+ and Na^+ homeostasis and better water status in maize exposed to salt stress (Zhang et al. 2016). Studies have shown that exogenous application of ABA mediates activation of its biosynthesis and inactivation of its degradation pathways to accumulate proline, which performs a protective function by scavenging free radicals in plants under salt stress (Jakab et al. 2005, Shevyakova et al. 2013). However, the role of ABA in salt acclimation process is unclear.

In the present study, the independent and combined effects of salt acclimation and ABA priming on the performance of photosynthetic electron system and salt tolerance in wheat were investigated. Our hypotheses were that: (1) ABA priming improves the photosynthetic electron transport and photosynthetic rate of salt acclimated plants; and (2) priming with ABA enhanced the salt acclimation induced salt tolerance in wheat.

MATERIAL AND METHODS

Experimental design. Selected seeds of winter wheat (cv. Lianmai 6) were grown in plastic pots (15 cm high, 25 cm in diameter), which were filled with 5 kg of clay soil. Four seeds were sown in each pot, and irrigated with tap water twice per week. At 4-leaf stage, the wheat plants were subjected to five treatments: C – non-stress control; ST – salt stress treatment (500 mmol NaCl for 3 days); AC + ST – salt acclimation (30 mmol NaCl for one week) + salt stress; ABA + ST – foliar ABA treatment (wheat plants were sprayed with 1 mmol ABA twice before salt stress) + salt stress; AC + ABA + ST – salt acclimation + foliar ABA treatment + salt stress. The plants were grown in a climate-controlled greenhouse at 26/18°C (day/night). The photosynthetic active radiation (PAR, 12-h photoperiod and > 500 μmol/m^2/s) supplied by sunlight and metal-halide lamps, and the relative humidity was 60–70%. The experiment was a randomized block design, with three replicates for each treatment. Each replication consisted of 3 pots.

Physiological traits. Just after the salt stress treatment, net photosynthetic rate (P_n) and stomatal conductance (g_s) were measured on the latest fully expanded leaf with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, USA) at a CO_2 concentration of 400 μmol/mol and photosynthetically active radiation of 1200 μmol/m^2/s. The relative chlorophyll content on the same leaf was measured with a SPAD 502 chlorophyll meter (Soil Plant Analysis Development, Minolta, Japan). The midday leaf water potential (LWP) was determined with a pressure chamber (Soil Moisture Equipment,

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Santa Barbara, USA). The relative water content (RWC) was measured on the latest fully expanded leaf according to Li et al. (2015). For measurements of sodium (Na) concentration, 100 mg leaf sample was incubated in 5 mL concentrated sulphuric acid completely digested with 30% H_2O_2 as catalyst. The digestive solution was transferred to 50 mL volumetric flask to the constant volume and diluted before the test with a TAS 986 atomic absorption spectrophotometer (Beijing Purkinje General Instrument, Beijing, China). Concentration of ABA was measured with ELISA following the protocol of Li et al. (2015). H_2O_2 concentration in leaf was measured by monitoring the absorbance of titanium peroxide complex at 410 nm following the methods of Li et al. (2013). The superoxide dismutase (SOD) activity was assayed by monitoring the inhibition of photochemical reduction of nitroblue tetrazolium, the activity of ascorbate peroxidase (APX) was measured following ascorbate oxidation by monitoring the decrease at 290 nm, and the catalase (CAT) activity was measured as described by Li et al. (2014a).

Chlorophyll *a* fluorescence. Fast chlorophyll *a* fluorescence induction curve (JIP curve) was measured on the same leaf as for the gas exchange measurement using the Plant Efficiency Analyzer (Pocket-PEA, Hansatech, Norfolk, UK). Before measuring, 30 min of dark adaptation of the leaf was applied. The data were processed and calculated using PEA Plus 1.04 (Bioenergetics Lab., Geneva, Switzerland).

Statistical analysis. The data was firstly tested for homogeneity of variance with boxplot and subjected to the one-way ANOVA using SigmaSTAT (V3.5, Systat Software Inc., San Jose, USA). Energy pipeline leaf model of phenomenological fluxes was performed with Biolyzer 3.0 (Bioenergetics Lab, Geneva, Switzerland, http://www.fluoromatics.com).

RESULTS AND DISCUSSION

The chlorophyll content (SPAD), leaf water potential and relative water content of wheat leaf were significantly reduced by salt stress (ST, 500 mmol NaCl), compared with a non-salt (C, 0 mmol NaCl) treatment (Figure 1). Salt-induced senescence involves a reduction of photosynthetic pigments (Ren et al. 2007). Here, salt acclimation (AC), ABA priming and their combination all increased leaf SPAD under salt stress. No significant difference in SPAD was found among AC + ST, ABA + ST and AC + ABA + ST. Under salt stress, the highest LWP and RWC were both observed in AC + ABA + ST, followed by AC + ST and ABA + ST, and the lowest values were found in ST. High salt concentrations in soil result in a decrease in water potential, which affects water availability (Jakab et al. 2005). The salt-induced osmotic stress reduces water absorption of roots and reduces leaf

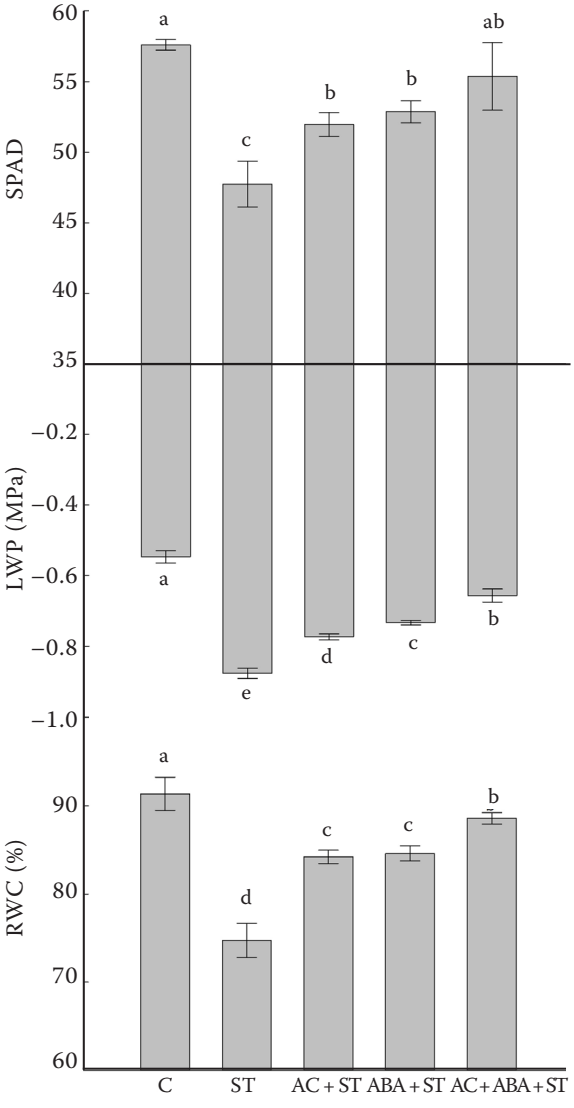

Figure 1. Effects of salt stress on chlorophyll content (SPAD); leaf water potential (LWP), and relative water content (RWC) of wheat plants acclimated with 30 mmol salt and primed with abscisic acid (1 mmol). Mean values ± standard error are shown (n = 3). C – non-stress control; ST – salt stress; AC – salt acclimation; ABA – foliar abscisic acid

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water status in wheat (Rahnama et al. 2010). In the present study, the reductions of RWC and LWP were significantly alleviated by single/combined treatments of salt acclimation and ABA priming. Also, the ABA priming enhanced the RWC and LWP of salt acclimated plants under subsequent salt stress. This indicated that ABA helps maintain a better water status of salt acclimated wheat plants under stress.

An initial response to salt stress is stomatal closure through the action of ABA (Garcia de la Garma et al. 2015, Janda et al. 2016). Enhanced ABA levels cause an increase in cytosolic Ca^{2+} concentration, hence leading to guard cell depolarization and stomatal closure (Blatt 2000). In the present study, stomatal conductance (g_s) was significantly depressed by salt stress, as compared to non-salt treatment (Figure 2). Higher g_s was found in salt-acclimated plants in relation to non-acclimated plants. ABA priming also increased the g_s of wheat plants under salt stress. However, the plants under the combination of salt acclimation and ABA priming (AC + ABA + ST) had lower g_s than AC + ST plants and ABA + ST plants. The net photosynthetic rate was significantly reduced by salt stress treatment. Both salt acclimation and priming with ABA enhanced the P_n of wheat plants under salt stress, and the plants in the combination treatment had higher P_n than in the single treatments. The results also showed that the plants under AC + ABA + ST had relatively lower g_s than AC + ST plants and ABA + ST plants; it indicated that priming with ABA improved the carbon assimilation and water use efficiency of salt-acclimated plants under salt stress. It has been well known that salt-induced inhibition of photosynthesis can be attributed to stomatal and non-stomatal limitations (Farquhar and Sharkey 1982, Sun et al. 2016). Thus, it suggested that ABA priming affected the photosynthesis of salt-acclimated wheat plants mainly due to the regulation of non-stomatal parameters.

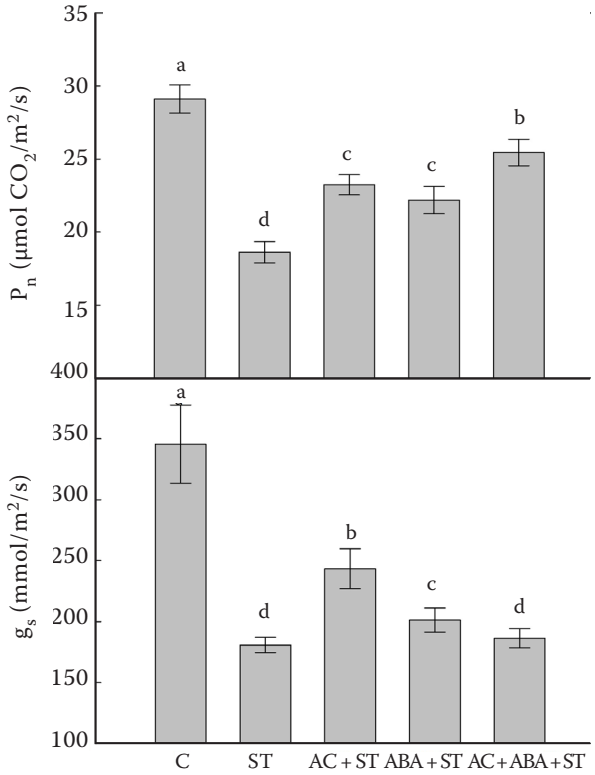

Figure 2. Effects of salt stress on net photosynthetic rate (P_n), and stomatal conductance (g_s) of wheat plants acclimated with 30 mmol salt and primed with abscisic acid (1 mmol). Mean values ± standard error are shown (n = 3). C – non-stress control; ST – salt stress; AC – salt acclimation; ABA – foliar abscisic acid

Stomatal control by ABA appears an efficient strategy to decrease water loss and the negative effects osmotic stress caused by salinity (Ren et al. 2007). In addition to osmotic constraint, high salt stress also imposes ionic stress on plants, mainly in relation to Na^+ accumulation (Munns 2002, Hassine and Lutts 2010). The salt stress treatment significantly increased Na^+ concentration in leaves compared with non-salt treatment (Figure 3). Lower Na^+ concentrations were found in AC + ST, ABA + ST and AC + ABA + ST compared with salt stress treatment (ST). In addition, ABA primed plants had relatively lower Na^+ concentration than the non-primed plants, regardless of whether they were salt acclimated. The ABA level in leaf was significantly enhanced by salt treatment. Interestingly, under salt stress, the highest ABA concentration was in AC + ABA + ST, following by that in ABA + ST, while the lowest value was found in ST. It has been reported that the *AtLOS5* (molybdenum cofactor sulfurase) overexpression in maize promotes ABA biosynthesis and accumulation, which activates ion transporter to regulate root ion fluxes, thus maintaining high cytosolic Na^+ and K^+ homeostasis under salt stress (Zhang et al. 2016). In accordance with this, reduced Na^+ concentration and increased ABA level were caused by the combination of salt acclimation and ABA priming. It indicated that priming with ABA enhanced the endogenous ABA concentration, which contributes to reduce Na^+ uptake and translocation in wheat.

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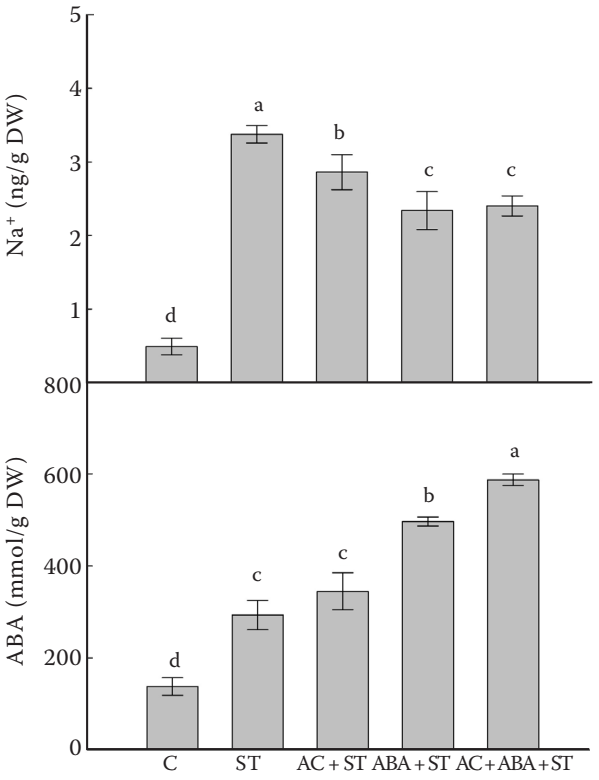

Figure 3. Effects of salt stress on concentrations of Na (Na^+), and abscisic acid (ABA) of wheat plants acclimated with 30 mmol salt and primed with abscisic acid (1 mmol). Mean values ± standard error are shown (n = 3). C – non-stress control; ST – salt stress; AC – salt acclimation; ABA – foliar abscisic acid; DW – dry weight

ABA has also been shown to trigger ABA-responsive genes and regulate activities of antioxidant enzymes (Hassine and Lutts 2010, Li et al. 2016). As a non-radical form of ROS, H_2O_2 inactivates enzymes by oxidizing their thiol groups leading to oxidative stress (Gill and Tuteja 2010). In the present study, H_2O_2 concentration was significantly increased by salt stress treatment, in relation to non-salt treatment (Figure 4). Compared with ST, the increment of H_2O_2 concentration was significantly less in the treatments of AC + ST, ABA + ST and AC + ABA + ST. This could be related to the enhanced capacity of oxygen scavenging systems caused by AC and ABA. The SOD activity was significantly enhanced by the combination of AC and ABA, while it was not affected by single AC or ABA treatment. However, the APX activity was significantly enhanced by AC + ST and AC + ABA + ST in relation to ST. A similar trend was found in CAT activity in wheat plants. It has been known that in the ROS scavenging systems, SOD catalyses the disproportionation of singlet oxygen ($^1O_2$) and

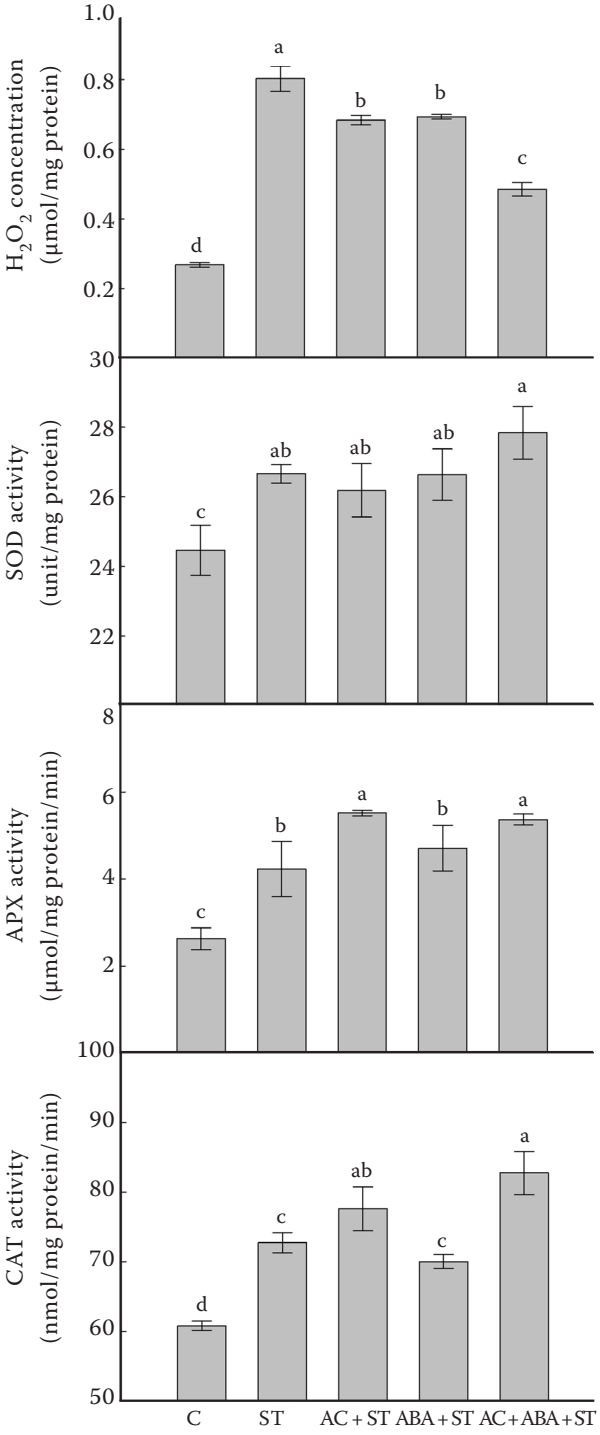

Figure 4. Effects of salt stress on concentrations of H_2O_2 and activities of superoxide dismutase (SOD); ascorbate peroxidase (APX), and catalase (CAT) of wheat plants acclimated with 30 mmol salt and primed with abscisic acid (1 mmol). Mean values ± standard error are shown (n = 3). C – non-stress control; ST – salt stress; AC – salt acclimation; ABA – foliar abscisic acid

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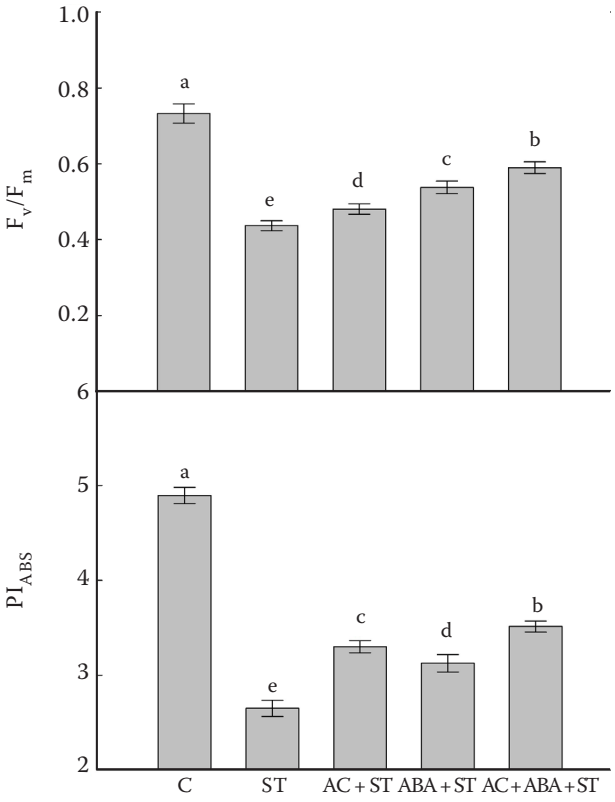

Figure 5. Effects of salt stress on maximum quantum yield of PSII (F_v/F_m) and performance index on absorption basis (PIABS) of wheat plants acclimated with 30 mmol salt and primed with abscisic acid (1 mmol). Mean values ± standard error are shown (n = 3). C – non-stress control; ST – salt stress; AC – salt acclimation; ABA – foliar abscisic acid

produces H_2O_2 (Li et al. 2014b). Then CAT and APX decomposes H_2O_2 to H_2O and O_2 (Li et al. 2014b). Here, the activities of CAT and APX were significantly enhanced by the combination of AC and ABA priming, indicating that decomposition of H_2O_2 was significantly improved by ABA priming in the salt-acclimated plants.

The maximum quantum yield of PSII (F_v/F_m) and performance index on absorption basis (PI_{ABS}) are two main parameters derived from the chlorophyll a fluorescence induction curves, which are widely used to investigate the photosynthetic electron transport under stress conditions (Kalaji et al. 2017, Zivcak et al. 2017). In this study, the F_v/F_m and PI_{ABS} were both depressed by salt stress, while they were relatively higher in ABA primed plants and salt-acclimated plants (Figure 5). Also, the highest values of these two parameters were found in the combination treatment of AC and ABA (AC + ABA + ST). The leaf model of phenomenological energy fluxes per cross-section was used to visualize the derived parameters (Li et al. 2014a). In the present study, the trapped energy flux per CS (TRo/CSo) and the electron transport in PS II cross-section (ETo/CSo) were reduced significantly in salt stress treatment, indicated by significantly smaller size of light blue and dark blue arrows in ST (Figure 6). ETo/CSo presented the reoxidation of reduced Q_A via electron transport over a cross-section of active and inactive reaction centres (RCs) (Li et al. 2014a). Also, it should be noted that TRo/CSo and ETo/CSo were significantly enhanced by salt acclimation and priming with ABA, and the highest values were obtained in their combination. The density of the active RCs, indicated as the number of open circles, was reduced by salt treatment but it was significantly increased by the combined treatment of AC and ABA. This suggested that ABA priming resulted in more active RCs in salt acclimated plants, hence improving the electron

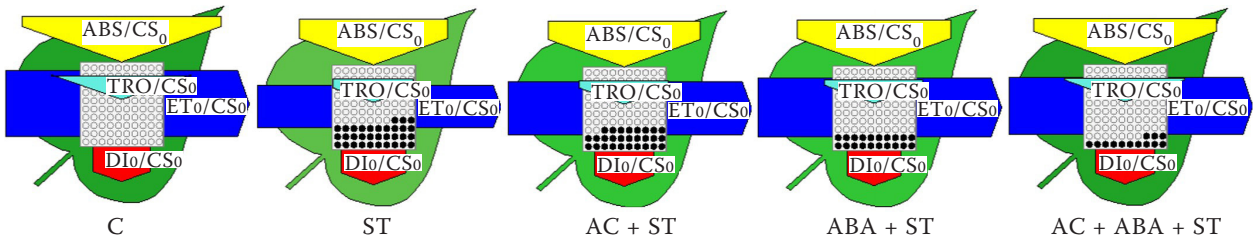

Figure 6. Energy pipeline leaf model of phenomenological fluxes (per cross-section, CS) in last fully expanded leaves as affected by salt stress. Data are means ± SE (n = 3). Each relative value is drawn by the width of the corresponding arrow, standing for a parameter. Empty and full black circles indicate, respectively, the percentage of active (QA reducing) and non-active (non QA reducing) reaction centres of PSII. TRO/CSm – trapped energy flux per CS; ETO/CSm – electron transport flux per CS; ABS/CSm – absorption flux per CS; DIO/CSm – non-photochemical quenching per CS. C – non-stress control; ST – salt stress; AC – salt acclimation; ABA – foliar abscisic acid

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transport under salt stress. The non-photochemical quenching (DIo/CSo), which was shown by the size of red arrows, was significantly higher in salt stress treatment as compared to non-salt treatment. However, there was no significant difference among ST, AC + ST, ABA + ST and AC + ABA + ST, indicating that ABA priming did not affect the non-photochemical quenching in salt-acclimated plants under subsequent salt stress.

In conclusion, priming with ABA (1 mmol) enhanced the salt acclimation induced salt tolerance via modulating leaf ABA concentration to maintain better water status in wheat. The ABA priming also drove the antioxidant systems to protect photosynthetic electron transport in salt acclimated plants against subsequent salt stress, hence improving the carbon assimilation in wheat.

REFERENCES

Blatt M.R. (2000): Cellular signaling and volume control in stomatal movements in plants. Annual Review of Cell and Developmental Biology, 16: 221–241.

Brestic M., Zivcak M., Kunderlikova K., Sytar O., Shao H.B., Kalaji H.M., Allakhverdiev S.I. (2015): Low PSI content limits the photoprotection of PSI and PSII in early growth stages of chlorophyll *b*-deficient wheat mutant lines. Photosynthesis Research, 125: 151–166.

Brestic M., Zivcak M., Kunderlikova K., Allakhverdiev S.I. (2016): High temperature specifically affects the photoprotective responses of chlorophyll *b*-deficient wheat mutant lines. Photosynthesis Research, 130: 251–266.

Bruce T.J.A., Matthes M.C., Napier J.A., Pickett J.A. (2007): Stressful 'memories' of plants: Evidence and possible mechanisms. Plant Science, 173: 603–608.

Cutler S.R., Rodriguez P.L., Finkelstein R.R., Abrams S.R. (2010): Abscisic acid: Emergence of a core signaling network. Annual Review of Plant Biology, 61: 651–679.

El-Hendawy S.E., Hassan W.M., Al-Suhaibani N.A., Refay Y., Abdella K.A. (2017): Comparative performance of multivariable agro-physiological parameters for detecting salt tolerance of wheat cultivars under simulated saline field growing conditions. Frontiers in Plant Science, 8: 435.

Farquhar G.D., Sharkey T.D. (1982): Stomatal conductance and photosynthesis. Annual Review of Plant Physiology, 33: 317–345.

Garcia de la Garma J., Fernandez-Garcia N., Bardisi E., Pallol B., Asensio-Rubio J.S., Bru R., Olmos E. (2015): New insights into plant salt acclimation: The roles of vesicle trafficking and reactive oxygen species signalling in mitochondria and the endomembrane system. New Phytologist, 205: 216–239.

Gill S.S., Tuteja N. (2010): Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry, 48: 909–930.

Hassine A.B., Lutts S. (2010): Differential responses of saltbush *Atriplex halimus* L. exposed to salinity and water stress in relation to senescing hormones abscisic acid and ethylene. Journal of Plant Physiology, 167: 1448–1456.

Jakab G., Ton J., Flors V., Zimmerli L., Me´traux J.-P., Mauch-Mani B. (2005): Enhancing *Arabidopsis* salt and drought stress tolerance by chemical priming for its abscisic acid responses. Plant Physiology, 139: 267–274.

Janda T., Darko É., Shehata S., Kovács V., Pál M., Szalai G. (2016): Salt acclimation processes in wheat. Plant Physiology and Biochemistry, 101: 68–75.

Janda T., Gondor O.K., Yordanova R., Szalai G., Pál M. (2014): Salicylic acid and photosynthesis: Signalling and effects. Acta Physiologiae Plantarum, 36: 2537–2546.

Kalaji H.M., Schansker G., Brestic M., Bussotti F., Calatayud A., Ferroni L., Goltsev V., Guidi L., Jajoo A., Li P.M., Losciale P., Mishra V.K., Misra A.N., Nebauer S.G., Pancaldi S., Penella C., Pollastrini M., Suresh K., Tambussi E., Yanniccari M., Zivcak M., Cetner M.D., Samborska I.A., Stirbet A., Olsovska K., Kunderlikova K., Shelonzek H., Rusinowski S., Baba W. (2017): Frequently asked questions about chlorophyll fluorescence, the sequel. Photosynthesis Research, 132: 13–66.

Li X.N., Cai J., Liu F.L., Dai T.B., Cao W.X., Jiang D. (2014a): Cold priming drives the sub-cellular antioxidant systems to protect photosynthetic electron transport against subsequent low temperature stress in winter wheat. Plant Physiology and Biochemistry, 82: 34–43.

Li X., Cai J., Liu F., Dai T., Cao W., Jiang D. (2014b): Exogenous abscisic acid application during grain filling in winter wheat improves cold tolerance of offspring's seedlings. Journal of Agronomy and Crop Science, 200: 467–478.

Li X.N., Cai J., Liu F.L., Li X.N., Cao W.X., Jiang D. (2014c): Physiological, proteomic and transcriptional responses of wheat to combination of drought or waterlogging with late spring low temperature. Functional Plant Biology, 41: 690–703.

Li X.N., Jiang H.D., Liu F.L., Cai J., Dai T.B., Cao W.X., Jiang D. (2013): Induction of chilling tolerance in wheat during germination by pre-soaking seed with nitric oxide and gibberellin. Plant Growth Regulation, 71: 31–40.

Li X.N., Tan D.-X., Jiang D., Liu F.L. (2016): Melatonin enhances cold tolerance in drought-primed wild-type and abscisic acid-deficient mutant barley. Journal of Pineal Research, 61: 328–339.

Li X.N., Topbjerg H.B., Jiang D., Liu F.L. (2015): Drought priming at vegetative stage improves the antioxidant capacity and photosynthesis performance of wheat exposed to a short-term low temperature stress at jointing stage. Plant and Soil, 393: 307–318.

Liu S., Li X., Larsen D.H., Zhu X., Song F., Liu F. (2017): Drought priming at vegetative growth stage enhances nitrogen-use ef-

doi: 10.17221/287/2017-PSE

ficiency under post-anthesis drought and heat stress in wheat. Journal of Agronomy and Crop Science, 203: 29–40.

Mehta P., Jajoo A., Mathur S., Bharti S. (2010): Chlorophyll *a* fluorescence study revealing effects of high salt stress on Photosystem II in wheat leaves. Plant Physiology and Biochemistry, 48: 16–20.

Munns R. (2002): Comparative physiology of salt and water stress. Plant, Cell and Environment, 25: 239–250.

Pál M., Janda T., Szalai G. (2011): Abscisic acid may alter the salicylic acid-related abiotic stress response in maize. Journal of Agronomy and Crop Science, 197: 368–377.

Pandolfi C., Azzarello E., Mancuso S., Shabala S. (2016): Acclimation improves salt stress tolerance in *Zea mays* plants. Journal of Plant Physiology, 201: 1–8.

Rahnama A., James R.A., Poustini K., Munns R. (2010): Stomatal conductance as a screen for osmotic stress tolerance in durum wheat growing in saline soil. Functional Plant Biology, 37: 255–263.

Ren H., Gao Z., Chen L., Wei K., Liu J., Fan Y., Davies W.J., Jia W., Zhang J. (2007): Dynamic analysis of ABA accumulation in relation to the rate of ABA catabolism in maize tissues under water deficit. Journal of Experimental Botany, 58: 211–219.

Shevyakova N.I., Musatenko L.I., Stetsenko L.A., Vedenicheva N.P., Voitenko L.P., Sytnik K.M., Kuznetsov VI.V. (2013): Effects of abscisic acid on the contents of polyamines and proline in common bean plants under salt stress. Russian Journal of Plant Physiology, 60: 200–211.

Sun Z.W., Ren L.K., Fan J.W., Li Q., Wang K.J., Guo M.M., Wang L., Li J., Zhang G.X., Yang Z.Y., Chen F., Li X.N. (2016): Salt response of photosynthetic electron transport system in wheat cultivars with contrasting tolerance. Plant, Soil and Environment, 62: 515–521.

Upadhyay S.K., Singh D.P. (2015): Effect of salt-tolerant plant growth-promoting rhizobacteria on wheat plants and soil health in a saline environment. Plant Biology, 17: 288–293.

Zhang J., Yu H., Zhang Y., Wang Y., Li M., Zhang J., Duan L., Zhang M., Li Z. (2016): Increased abscisic acid levels in transgenic maize overexpressing *AtLOS5* mediated root ion fluxes and leaf water status under salt stress. Journal of Experimental Botany, 67: 1339–1355.

Zivcak M., Brückova K., Sytar O., Brestic M., Olsovska K., Allakhverdiev S.I. (2017): Lettuce flavonoids screening and phenotyping by chlorophyll fluorescence excitation ratio. Planta, 245: 1215–1229.

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